

# Systematic position and palaeoecology of a cavity-dwelling trilobite, *Ityophorus undulatus* Warburg, 1925, from the Upper Ordovician Boda Limestone, Sweden

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**Abstract.** The high level systematic position and autecology of the Upper Ordovician cavity-dwelling trilobite *Ityophorus undulatus* is discussed. The lectotype is here selected from syntypes. The Late Cambrian family Loganellidae Rasetti, 1959 appears to contain the ancestors of this species. *Ityophorus* is compared with the closely related Middle Ordovician trilobite *Frognaspis* to pick out the stable characters. These are the yoked free cheeks, the wide cephalic doublure in combination with a distinct narrow cephalic rim, pygidial pleural and interpleural furrows, and a smooth mesial part of the inner cephalic doublural margin (lack of an embayment of the hypostomal suture). Because of the presence of several characteristics unique to the two, they are best attributed to a subfamily Ityophorinae, which is interpreted as a relict group of the Loganellidae. The discussion of the autecology is based on the structural relationship of the mouth opening and position of basal podomeres in relation to the cephalic margin, and on the functional morphology of terrace lines on the brim margin. The appendages appear to have been long to reach the substrate. The cephalon appears to have held the body rigidly by means of the terrace lines. This made it possible for the animal to use its appendages freely, for instance, in scratching the substrate. Some cavities in the present study area show evidence of a gel-like consistency of the cavity walls, which best fits the behavior mentioned above. *Ityophorus* is interpreted to have been an animal adapted to cavities rich in bacterial mats, on which it may have fed.

**Key words:** cavity dwelling, *Ityophorus undulatus*, life habit, Loganellidae, structural relationship, Trilobita, yoked free cheeks.

## Introduction

The term “cryptic habit” denotes an adaptations into a buildup environment, which usually provides cohesive substrates with the potential to provide cavities. Caves in recent reefs, which offer spaces for cryptic modes of life, occasionally are dominated by sponges and cryptic bacteria (Reitner, 1993). With these, bivalves, gastropods and arthropods form cryptic biotopes. From a classificatory point of view, some cavity-dwelling metazoans appear to be phylogenetically relict groups (relict biota), or groups which retain primitive morphological characters (Hayami and Kase, 1996; Hobbs, 2001). This trend should have been characteristic also of ancient cavity dwellers in buildups, although no vagile metazoan fossil group has ever been recognised as a “relict group” so far.

The Upper Ordovician minute trilobite species *Ityophorus undulatus* Warburg, 1925, which is of uncertain position in high-rank systematics (Kaesler, 1997, p. 302), is commonly found in patches of internal sediment in

autochthonous taphonomical conditions (Suzuki and Bergström, 1999, fig. 10), commonly associated with microgastropods. The sediment is characteristic of the “stromatolite cavity” system which is a common sedimentary structure in Palaeozoic carbonate mud mounds. Thus Suzuki and Bergström (1999) concluded that the present species was a cavity dweller. This rare mode of occurrence, which is defined correctly as a cavity setting, offers us an unusual chance to examine if a fossil species of cryptic habit has a similar mode of adaptation to recent examples or not.

The aims of the present study are to examine the high-rank systematic position of *Ityophorus undulatus*, to present an example of morphological transformations in a trilobite caused by environmental pressure, and to discuss the autecology from functional and sedimentological points of view.

## Geological setting

*Ityophorus undulatus* occurs in the Upper Ordovician Boda Limestone, Siljan district, Sweden. This unit

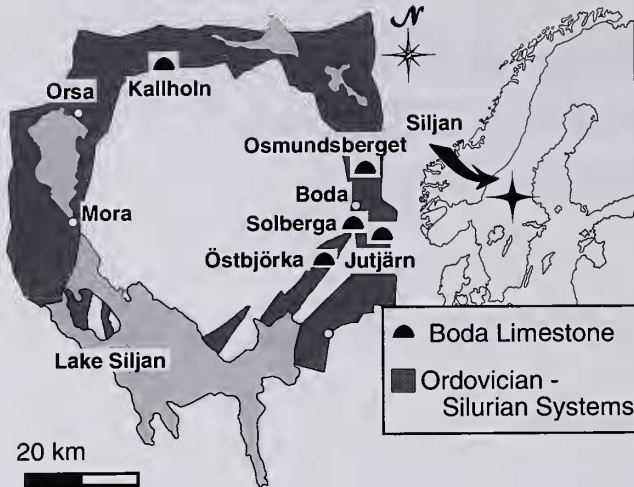


Figure 1. Locality map of some Boda Limestone bodies.

consists of a set of carbonate buildup masses of which now up to 20 are known in the Siljan district of Sweden (Figure 1; Jaanusson, 1979). The thickness and the diameter of an isolated Boda Limestone body are said to be about 100-140 m and up to over 1 km, respectively (Jaanusson, 1982). However, my own observations and calculations based on a topographic map indicate a maximum size more or less half the dimension mentioned. The facies is massive pure limestone without obvious bedding, but with frequent open space structures such as stromatactis cavities and synsedimentary dykes. *Ityophorus undulatus* is commonly found with internal sediment in relatively large open space structures. On the rim of these, a unique type of open space structure is often recognised, shown in Figure 2B. Microscopically, internal sediment is dominated by peloids, and the host sediment is micritic (Figure 2D). In case of the Boda Limestone, "normal" stromatactis structures differ considerably both macroscopically and microscopically (Figure 2A, D; or readers are referred to Pratt, 1995, p. 63, fig. 14G). The internal sediment in stromatactis cavities and host sediments of the cavity system is mostly microcrystalline, and peloids are rare. The transversely elongate cavity system with peloids which is similar in construction to that shown in Figures 2B and 2D is generally classified as "zebra cavity of laminoid or flat stromatactis type" (for definition, see Monty, 1995, p. 25), and is interpreted as originating by the decay of superposed thin sheet-like microbial mats (Pratt, 1982).

### Systematic description

The present species was originally described in detail by Warburg (1925, p. 229). General characters and new observations are presented below.

Genus *Ityophorus* Warburg, 1925

Type species.—*Ityophorus undulatus* Warburg, 1925

*Ityophorus undulatus* Warburg, 1925

Figure 3

*Ityophorus undulatus* Warburg, 1925, p. 229, pl. 11, figs. 40-43; Moore, 1959, p. O430, fig. 333; Nikolaisen, 1965, p. 237.

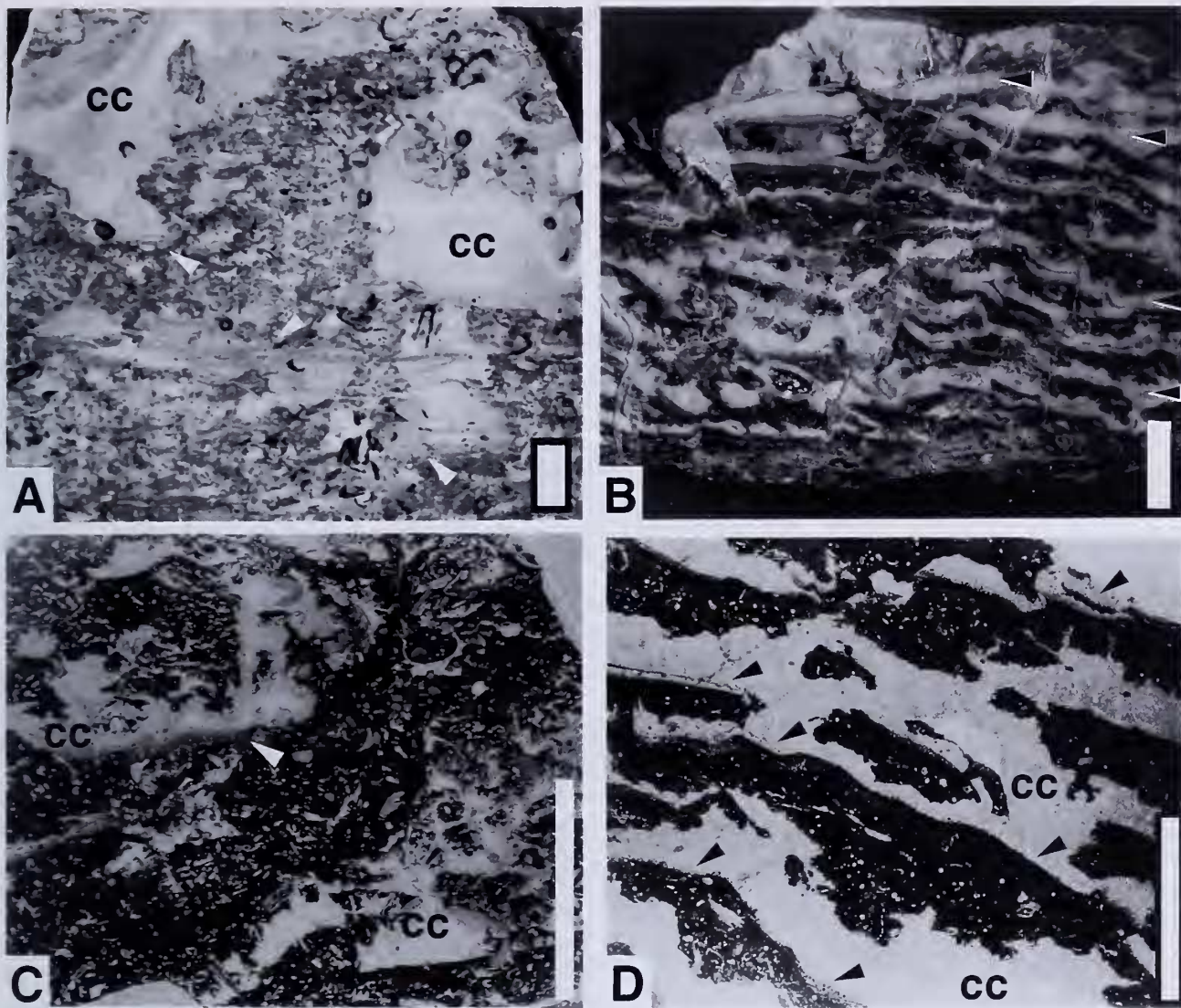
*Types*.—3 syntypes, PMU D194 (Warburg, 1925, pl. 11, fig. 40), PMU D195 a, b (Warburg, 1925, pl. 11, fig. 41) and PMU D196 (Warburg 1925, pl. 11, figs. 42, 43), are housed in the Palaeontological Institute, University of Uppsala. PMU D196 is here selected as the lectotype.

*Type locality*.—Boda Limestone, a buildup mass in Kallholn, Dalarna, Sweden. The stratigraphic level within the mass is unknown. The range of the species is likely to correspond to the Cautleyan to Rawtheyan stage of the Ashigill series, and not the Hirnantian.

*Repository*.—All the specimens figured herein are housed in the Swedish Natural History Museum, Stockholm, with "RM" numbers.

*Description*.—The entire exoskeleton is ovate in outline (Figure 3A). Its entire length seldom exceeds 1 cm. The cephalon occupies about half of the length, sagittally. The axis is fairly convex, and almost half of a circle in cross-section.

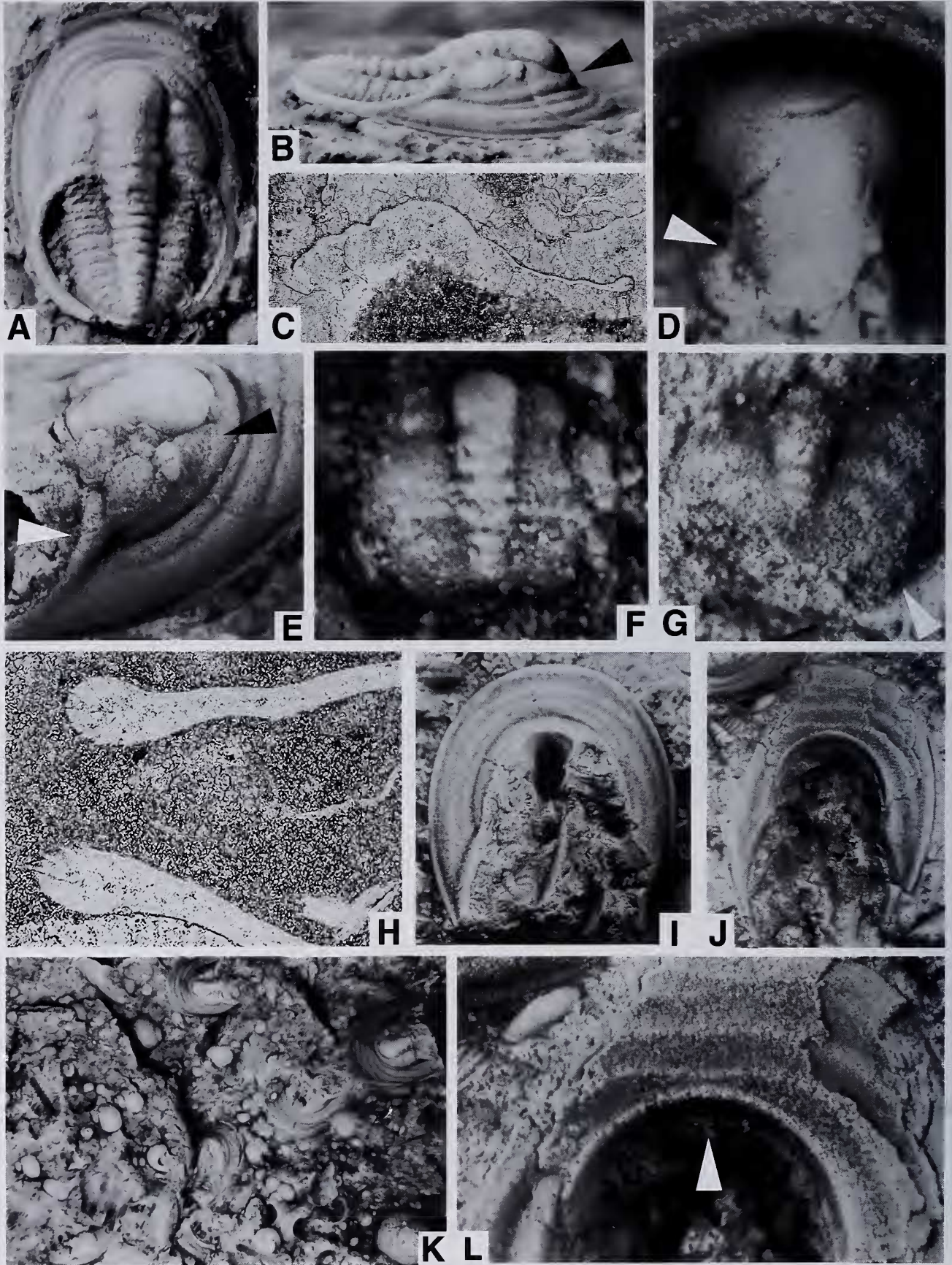
The cephalon is horseshoe-shaped (Figure 3A) and strongly convex (Figure 3B). The maximum length including the genal spine is about twice the sagittal length and almost equal to the length of the entire body. The genal angle is acute. The long genal spine curves evenly posteriorly and adaxially. The width of the spine is almost constant throughout. Its posterior end is situated more or less at the level of the posterior end of the pygidium. The anterior cephalic rim, which is narrower and less convex than the posterior cephalic border, disappears where it meets the genal spine. Thus, the genal spine is seemingly an extension of the cephalic posterior border. The glabella is cylindroid in profile and expands slightly anteriorly. It is strongly convex transversely. Three pairs of glabellar furrows are recognised. The 2S and 3S furrows are short and extend more or less transversely. Their length is about one fourth the width of the glabella. The 1S furrow is longer than the 2S and 3S furrows. It is directed about 45° posteriorly from a transverse line. It becomes wider adaxially. Probably the furrow is bifurcated adaxially, but the specimens are too small for a definite observation. The eye ridge is short but strongly convex, and distinctly set off from the surroundings. It extends transversely in front of the level of the 3S glabellar furrows. The length of the eye ridge roughly equals the distance between the 2S



**Figure 2.** Macro- and microfacies of the Boda Limestone. **A.** Polished slab of the core facies, vertical section. White arrows indicate laminated internal sediment. **B.** Polished slab of the "zebra cavity", sampled from the rim of an open space structure. Vertical section. Transversely continued white area pointed by black arrows are cavity systems. **C.** Microfacies of the core facies. Matrix is rich in bioclasts. White arrow indicates microcrystalline internal sediment. **D.** Microfacies of the zebra cavities. Black arrows point to peloidal internal sediment. All white scales are 1 cm. CC stands for cavity filling cement.

and 3S furrow. There may be eyes, as described by Warburg (1925, p. 230). However, the structure described as the eye may be vestigial since it is not proven that there is a visual surface. The possible visual surface forms half a sphere. A median occipital tubercle is present anteriorly on the occipital ring. The peripheral genal area is steeply inclined. Five furrows extend in parallel with the narrow cephalic rim (Figure 3A). The outermost one is the furrow of the cephalic rim. The innermost one extends laterally and posteriorly from the anterior end of the glabella (Figure

3B, E; black arrows). The area between these furrows is moderately convex. The brim, here defined as the area outward of the fourth furrow described above, is broad. The undulating brim has a general dip sagittally from the inner to the outer margin of around 30° (Figure 3C). The dip gradually becomes steeper backwards to about 60° laterally. The facial sutures are of opisthoparian type. Their anterior branches enclose a parabolic anterior part of the cranidium (Figure 3E). The posterior branch extends obliquely backwards to cross the cephalic posterior border



at a right angle (Figure 3E; white arrow). The free cheeks are fused into a single unit, because no furrows or gaps are recognised on the cephalic doublure (compare dorsal and ventral cephalic views in Figure 3I, J, respectively). The doublure closely follows the shape of the brim, and the space between the two is very narrow (Figure 3C). The doublure is wide (Figure 3C, J, L). The interior edge of the doublure (Figure 3L; white arrow) is situated below the innermost parabolic furrow in the cephalon, which is indicated by black arrows in Figure 3B, E. The cephalic doublure has three or four parabolic furrows which are almost parallel to the cephalic margin (Figure 3J). An interior part of the doublure, between the fourth and fifth parabolic furrow mentioned above, is steeply inclined and distinctly set off from the surrounding. Thus the cephalic doublure morphology is quite similar to the lower lamella of harpids.

In the cephalic rim, terrace lines with an asymmetrical cross-section are recognised on both the dorsal and ventral side (Figure 3H). The steep surfaces of the ventral terrace lines face dorsally, whereas they face ventrally in the dorsal ones (for detail, see Figure 5).

The hypostome is situated just below the glabella (Figure 3I). Its anterior margin must have been in contact with the cephalic doublure mesially. Three specimens among hundreds of cephalons show the same position of the hypostome. Thus the described position of the hypostome should be original. The length of the hypostome is 55% of that of the glabella (Figure 3D). It is strongly convex transversely. The maximum length is about 1.3 times longer than the maximum width. An anterior wing is relatively long (exsag.) and evenly inclined dorsally. The distal part of the wing is broadly rounded. The anterior margin is slightly depressed medially. The lateral border is narrow and short. The border furrow extends from the level of the posterior end of the anterior wing to four-fifths of the anterior end of the hypostome. The shoulder is triangular in shape and horizontally extended (Figure 3D; white arrow). The posterolateral corner of the central body is angulate. The posterior margin is convex without a border. No distinct boundary separating the anterior and the posterior lobes is recognised. The central body is longitudinally elliptic in shape.

The thorax consists of six segments (Figure 3A). The axis gradually becomes narrower backwards. The ratio between axial and pleural widths ranges from 1 to 1.2 from in front to the rear. The pleurae extend almost straight transversely except for the posteriormost two segments, in which the pleurae distal to the geniculation curve moderately backwards. A distinct pleural furrow is present. It extends almost parallel to the anterior and posterior margins of the segment.

The pygidium is wide (Figure 3A). The maximum width/length ratio is about 1.9. Six axial rings and five pairs of pleural ribs are discernible. Distal to the fulcrum, pleural ribs and furrows curve gently backward. Pleural and interpleural furrows lie parallel with each other. The posterior end of the axis is obscure. It gradually dies out posteriorly. A narrow flattened border is present.

Specimens of a younger growth stage, a meraspid degree? (Figure 3F), and a transitory pygidium (Figure 3G) are available. Both specimens are found along with adult specimens in internal sediment. No other trilobite species is recognised in this sediment. The former specimen (Figure 3F) is most probably a moult, because it lacks the entire free cheek unit. The glabella is proportionally narrower than in the adult. The 2S furrow differs in its course from that of the adult. The abaxial end of the furrow does not reach to the axial furrow. The furrow is directed posteriorly and adaxially in the young specimen, but transversely in adults. The axial ring of the first thoracic segment is seen posterior to the cephalon. A distinct eye ridge is present. Its proportion and position in relation to the glabella is almost the same as in an adult specimen. A most notable feature is the facial suture course. The anterior branch is not parabolic as in adult specimens, but extends straight forwards. The transitory pygidium seems to have a spiny margin (Figure 3G; white arrow). The posterior extremity of the axis ends well in front of the margin. The preservation is not good enough to permit further observations.

*Remarks.* — Previously, Warburg (1925, p. 231) described the genal spine of the present species as being a short pointed spine. Because of the minute size of the species, it tends to be broken. In most of the cases the genal spine is recognised as a concave mould.

← **Figure 3.** *Ityophorus undulatus* Warburg, 1925. **A.** Complete exoskeleton, dorsal view.  $\times 18$ . Jutjärn. RM Ar 56890. **B.** Same, lateral view.  $\times 17$ . Black arrow points to the furrow, below which the inward edge of the doublure is situated. **C.** Exsagittal or sagittal section of the cephalon.  $\times 39$ . Jutjärn. RM Ar 56891. **D.** Hypostome, ventral view.  $\times 54$ . Jutjärn. RM Ar 56892. White arrow points to the posterior wing, which is partly broken. **E.** Cephalon, oblique lateral view showing curving facial suture course.  $\times 15$ . Locality unknown. RM Ar 56893. White arrow points to the termination of the posterior branch of the facial suture. Black arrow to the furrow, below which the inward edge of the doublure is situated. **F.** Fairly young individual.  $\times 70$ . Jutjärn. RM Ar 56894. **G.** Fairly young pygidium.  $\times 65$ . Jutjärn. RM Ar 56895. White arrow points to pygidial spine. **H.** Magnified brim in cross section.  $\times 150$ . The lower brim of the two is upside down. Jutjärn. RM Ar 56896. **I.** Ventral mould of hypostome and cephalic brim, dorsal view.  $\times 16$ . Specimen is in the same slab as G. **J.** Cephalic doublure, ventral view.  $\times 12$ . Same slab as E. **K.** Occurrence pattern with microgastropods.  $\times 4$ . Same slab as E. **L.** Magnified cephalic doublure, ventral view.  $\times 45$ . Specimen same as J. White arrow points to the inner edge of the cephalic doublure.

### Systematic position of *Ityophorus undulatus*

#### Morphological characters of *Ityophorus* and *Frognaspis*

For more than a half century, opinion on the high-rank classification of the present genus was far from a clear consensus. First, Warburg (1925) made a new family Ityophoridae consisting of only the present genus. Later in Moore (1959), the species was doubtfully classified as a member of the Trinucleina Swinnerton, 1915, of the order Ptychopariida without any demonstrated evidence. It is clear that the convex cephalon with horseshoe outline is just a superficially similar to a trinucleid cephalon. Nikolaisen (1965) described a new species, *Frognaspis stoermeri*, which is closely related to the present species, from the Middle Ordovician of Norway, and classified it into the Ityophoridae. Furthermore, he implied a neotenic development of the present species from *Frognaspis stoermeri*. As will be discussed in a later paragraph, *Frognaspis stoermeri* shares fairly many characters with the present species. The suggestion of a close relationship between the two is therefore convincing. However, Nikolaisen did not tackle the problem of the position of Ityophoridae. Fortey (1997) also gave up and simply stated that the family belongs to the Ptychopariida Swinnerton, 1915.

Before examining the high-rank systematic position of the present species, we must understand how the unique morphology evolved in the phyletic lineage. Since *Ityophorus undulatus* preserves characters seen in young individuals of *Frognaspis stoermeri*, the heterochronic evolution of the former from the latter is worth consideration. After comparison of the two, we can sort out a "heterochronic polish". Then we can define stable characters and infer the ancestral conditions of characters which differ between the two. In addition, one has to remember what kind of morphological changes would arise in a shift to cavity-dwelling habits in modern arthropods.

Characters shared between *Ityophorus undulatus* and *Frognaspis stoermeri* are as follows:

- 1) wide cephalic brim.
- 2) facial suture course.
- 3) distinct furrows in the cephalic doublure.
- 4) small eyes.
- 5) fairly wide cephalic doublure with distinct narrow cephalic rim.
- 6) free cheeks forming single unit.
- 7) distinct pleural furrow (known only from the pygidium in the latter species).
- 8) narrow flattened pygidial rim.
- 9) pygidial pleural ribs distal to the geniculation extend obliquely backwards.
- 10) hypostomal morphology.
- 11) directions of pleural tips in the thorax.

- 12) cephalic doublural margin smoothly rounded mesially (no embayment for the hypostomal suture). Since the mesial part of the inner margin of the doublure is below the anterior extremity of the glabella, the hypostome should be attached to the doublure medially.

Characters which are not shared by the two species are:

- 1) glabellar profiles (expanded in *Ityophorus*).
- 2) glabellar furrows (deepened adaxially and 1S furrows faintly connected over midline in *Frognaspis*).
- 3) number of segments in the pygidium.
- 4) ornaments on dorsal surfaces.

The characters 1) and 2) in *Ityophorus* are apparently derived from younger growth stages of *Frognaspis* (see Nikolaisen, 1965, pl. 3, fig. 4). The inferred ancestral conditions of the two characters should thus be represented in the adult stages of *Frognaspis*.

The ancestral glabellar character 1) should be preserved in the adult stage of *Frognaspis*. This is because the glabellar profile in *Ityophorus* is fairly similar to a younger stage of *Frognaspis* (Nikolaisen, 1965, p. 243). Thus the ancestral group should have had an anteriorly tapering glabella, and possibly the 1S furrows may have been connected mesially (non shared character 2). The latter situation is recognised in *Frognaspis*.

Determining the ancestral condition of character 3) is difficult. This is because the adult number of pygidial segments is, in general, related to the number of thoracic segments. Unfortunately, the exact number of thoracic segments is not known in *Frognaspis*. I can only say that the ancestral condition of the number of segments in the pygidium may vary between species in the high-rank group, in which the two species belong.

Concerning character 4), since the exoskeletal ornament pattern is unstable among the genera in some family groups (e.g., Styginidae), we should hesitate to use that character in determining the high-rank systematic position. In general, recent cavity-dwelling organisms are equipped with specialized sensory organs. Especially in cavity-dwelling arthropods, the appendages tend to be long, which increases the area for the number or the size of sense organs (Culver, 1982, p. 17). Coarse tubercles on the exoskeletal surface in trilobites are generally understood as sensory ducts (Osmólska, 1975, p. 203). As will be discussed in a later paragraph, *Ityophorus* must have had long appendages, so the animal had the potential to equip its appendages rather than the dorsal exoskeleton richly with sensory organs. Thus smoothing of the dorsal exoskeletal surface may be a result of adaptation inhabiting cavities.

#### Discussion of systematic position of *Ityophorus*

I first try to narrow down candidate ancestral groups of *Ityophorus* from other groups with yoked free cheeks.

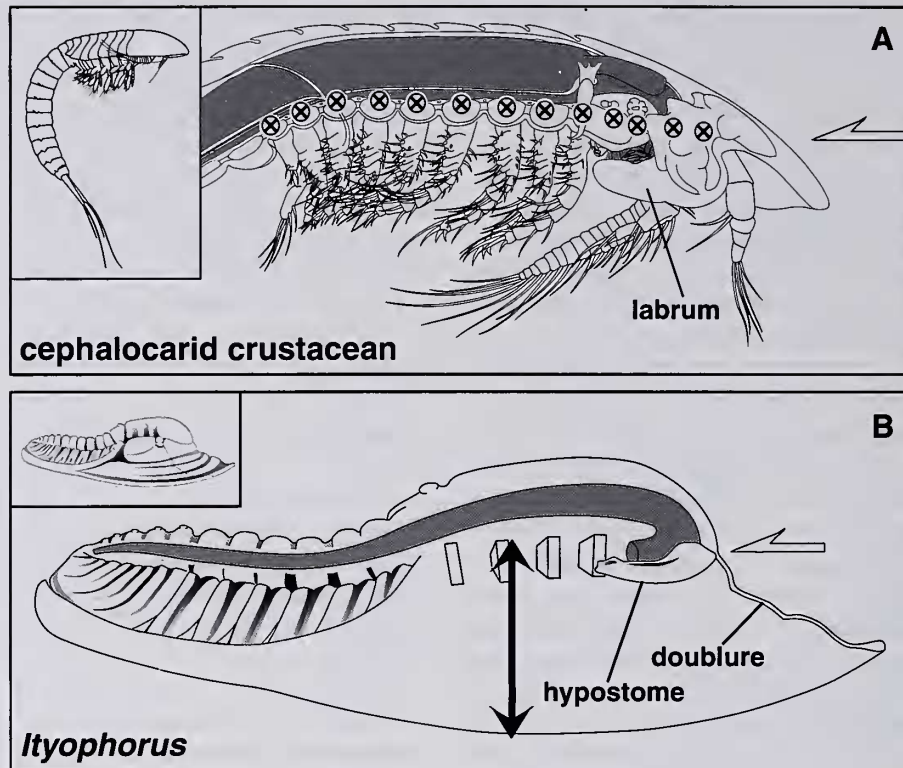
Next, I judge the possible relationships based on other characters such as ventral morphology, facial suture type, and pygidial morphology.

Trilobite groups which possess yoked free cheeks are bathynotids and conocoryphids from the Lower to Middle Cambrian, Nileidae, Phacopida, Trinucleina, Harpina, Olenidae, Hypermecaspididae, some species of Dikelocephalidae such as *Dikelocephalus retrorsus*, Loganellidae, some species of Dikelocephalinidae (readers are referred to *Dactylocephalus latus* (Peng, 1990a, pl. 9, fig. 8) and *Ciliocephalus angulatus* (Peng, 1990b, pl. 17, fig. 3)), Harpididae and Entomaspididae. Of these, the Lower Cambrian groups are so different in several characters such as facial suture courses, pygidial morphology and ventral cephalic characters, that a phylogenetic relationship with *Ityophorus* or *Frognaspis* is most unlikely. Harpina and conocoryphids (marginal suture), Harpididae (marginal or characteristic proparian suture), Phacopida (proparian suture) are profoundly different in their facial suture types from that of *Ityophorus*. Among the rest, the Entomaspididae have a characteristic pygidial morphology (a narrow upturned (geniculated) border or stubby spines in front of a continuous pygidial rim: Ludvigsen *et al.* 1989, p. 47) which is unlikely of the ancestor of *Ityophorus*. Most of the Trinucleina do not have eyes with dorsal facial suture except some genera such as *Orometopus* which has opisthoparian facial sutures. However, the overall morphology, especially the pygidial morphology of trinucleid type is quite different from the *Ityophorus* pygidium with distinct border and posteriorly curved pleural and interpleural furrows. The Nileidae have a characteristic hypostome, cephalic and pygidial morphology, large eyes with no eye ridges, more or less straight pygidial furrows, all of which are unlikely in a relative of *Ityophorus*. The Olenidae and the Hypermecaspididae have yoked free cheeks. In the case of olenids and hypermecaspidids with a wide preglabellar field, the cranidium is similar in outline and the cephalic doublural margin smoothly rounded mesially as in *Ityophorus*, but the hypostomes become natant. Since the hypostome of *Ityophorus* and *Frognaspis* must have attached mesially to the cephalic doublural margin (shared character 12), their ancestor should have possessed this mode of hypostomal attachment. Moreover, the pleural and interpleural pygidial furrows of the Olenidae and the Hypermecaspididae extend obliquely posteriorly in a more or less straight way, which is different from the situation in *Ityophorus*. Therefore, a phylogenetic relationship between the Olenidae and *Ityophorus* is unlikely.

Other candidates are the Dikelocephalidae, Dikelocephalinidae and Loganellidae. Some species of the former two families, although not all, possess yoked free cheeks with a wide cephalic doublure. The pygidial morphology is also

fairly similar between them. The Dikelocephalidae and the Loganellidae were extinct before the Cambrian-Ordovician transition, whereas the Dikelocephalinidae persisted beyond that boundary (Öpik, 1967, p. 254). One could therefore think that the third group, the Dikelocephalinidae, might contain the ancestor of *Ityophorus*. Classifying the Dikelocephalinidae is usually difficult, because most of the characters are too general to be diagnostic (Fortey and Chatterton, 1988, p. 209). However, the pygidium of Dikelocephalinidae has posteriorly curved pleural furrows but not interpleural furrows whereas *Ityophorus* has both. Thus, Dikelocephalinidae should not be related to *Ityophorus*. The Dikelocephalidae and the Loganellidae have interpleural furrows in their pygidia. However in the former, an embayment is present mesially in the cephalic doublure for an attachment of the hypostome. In contrast, the Loganellidae have a mesially smooth outline of the cephalic doublure (Moore, 1959, p. O333) which is concordant with the ventral cephalic morphology in *Ityophorus*. Below I discuss the phylogenetic relations between the Loganellidae, and *Ityophorus* and *Frognaspis*.

There are several shared characters between the Loganellidae and the two species such as the shared characters between *Ityophorus* and *Frognaspis* (1, 2, 5, 6, 7, 8, 9) and 11) listed above. Furthermore the characters of the inferred ancestral conditions which are listed as non-shared characters between *Ityophorus* and *Frognaspis* (1) and 2) fit well to this family. Generally, in species with the free cheeks in a single unit and a wide doublure, the cephalic rim [called a "border" in Fortey and Chatterton 1998: fig. 6, readers are referred to Whittington and Kelly (1997, p. 315) for the terminology of the "border" and "rim"] is of fairly low convexity (e.g., Fortey and Chatterton, 1988, fig. 6). Nikolaisen (1965, p. 237) stressed the differences in eye size and the hypostomal morphology in species between loganellids and *Frognaspis* or *Ityophorus*, but the reduction of eye size is a common feature in organisms adapted to cavities (Humphreys, 2000, p. 4). Anteriorly in the hypostome of *Ityophorus* and *Frognaspis*, there is a unique longitudinal median groove (Figure 3D; Nikolaisen, 1965, pl. 3, fig. 6). The groove structurally corresponds to the median longitudinal groove or depression (see Nikolaisen, 1965, pl. 2, figs. 1, 3; pl. 3, figs. 1, 2) anteriorly in the *Frognaspis* glabella. In general, species with yoked free cheeks (e.g., *Cloacaspis senilis*: see Fortey, 1974, pl. 10, fig. 6) may or may not possess a similar longitudinal glabellar groove or depression. If present, the longitudinal groove in the glabella tends to be more weakly impressed in older growth stages (Fortey, 1974, fig. 6). Thus the groove is more or less an embryonic character. Hence the two latter genera are most likely descended from a species of the Loganellidae. However, there are still several facts



**Figure 4.** A. Schematic drawing of cephalocarid crustacean showing the structural relationship in basal appendage joints (represented as "X" in a circle), digestive tract (grey area), labrum and basal podomere. Positions of the joints are situated above the level of the mouth opening. Modified from Sanders (1963: fig. 4) and Hessler and Elofsson (1992: fig. 3). B. Schematic drawing of *Ityophorus undulatus* showing structural relationship in inferred digestive tract (grey tube), hypostome and basal podomeres (represented as bricks). White arrows indicate dorsoventral level of mouth openings. Black double arrow indicates minimum distance between basal joints of appendages and the substrate.

which may differentiate *Ityophorus* and *Frognaspis* from typical Cambrian loganellids: 1) the two are Middle to Late Ordovician trilobites, 2) the body size of the two has undergone considerable shrinking, 3) the presence of crescentic furrows in the doublure (shared character 3) in the two species, but not in Cambrian loganellids. Therefore, the two genera are best accounted for as a subfamilial group of the Cambrian Loganellidae. *Ityophoridae* Warburg, 1925, including *Frognaspis* and *Ityophorus*, is therefore downgraded to a subfamily *Ityophorinae* Warburg, 1925, of the family Loganellidae Rasetti, 1959.

The *Ityophorinae* now appears to be a relict of the Late Cambrian group. Since growth stages are unknown in most fossil arthropods, how the *Ityophorinae* had evolved from a loganellidae as becomes vague. Recent animals, "progenetic evolution" is quite common as part of a cryptic adaptation, and the considerable size decrease of the *Ityophorinae* in comparison with the Loganellidae may be one indication of "progenetic evolution".

#### Functional morphology of *Ityophorus undulatus*

The present species had attained a body with apparently a "snow-shoe" effect, which increases the area of the animal substrate interface and prevents the animal from sinking into the substrate. A parallel is seen in harpid trilobites, although previous functional studies of these were restricted to the function of their characteristic brim. Unfortunately, we have no data on appendages in *Ityophorus* or harpid trilobites. It may be worth trying to infer the length and use of the legs from the space relationships between the probable attachment of the legs and the head shield, particularly its margin. This may give some hint of the mode of life.

#### Elevation of leg insertion over substrate

The hypostome of *Ityophorus* is oriented horizontally (Figures 3I, 4). This means that the mouth opened backwards, and not downwards. Recent crustaceans such as cephalocarids and notostracans a structure similar to the trilobite hypostome plus associated soft tissue is present, al-



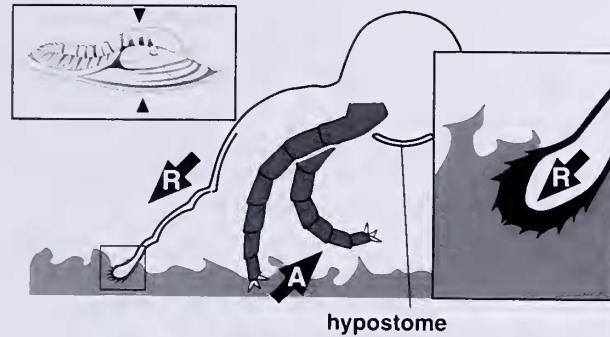
though it is not homologous. This is the "labrum". In a crustacean with a labrum the digestive tract first extends forwards from the mouth. The tract then flexes in the head and continues backwards (Figure 4; see grey area in the cephalocarid), extending more or less straight to the anus. The digestive tract in *Ityophorus* should have followed the same course as in the cephalocarid crustacean (Figure 4; *Ityophorus* with digestive tube in grey). Actual evidence on such a digestive course in trilobites is reported in phacopid (Stürmer and Bergström, 1973, pl. 20) and trinucleid trilobites (Šnadjr, 1987, fig. 3).

In case of a crustacean with the mouth opening backward, there is an important structural relationship between the dorsoventral positions between the labrum and the basal podomeres. Since the mouth is directed backwards, food particles have to be transported mechanically (handled by appendages) or indirectly (handled by food collecting wave created by appendages) from back to front *via* the midventral line. For transporting the food particles, the "labrum" and mouth must be situated below the level of the midventral line posterior to the labrum. Since the line is higher than the labrum and the mouth, the basal podomeres, which are attached to the axial body, automatically are at more or less the same horizontal level as the mouth opening. Such a relationship is seen in three-dimensionally preserved *Ceraurus* (Walcott, 1881, pl. 2, figs. 1-3). In *Ityophorus*, the spatial relationship between hypostome and basal podomeres appears to have been identical (see white arrow in Figure 4B). Therefore, the basal podomeres must have been situated fairly high relative to the cephalic margin (Figure 4). This configuration forced the animal to develop long appendages simply to reach the substrate. As discussed earlier, this condition is a common feature in cavity-dwelling arthropods, and *Ityophorus* could probably rest with the brim on the substrate without using its appendages. This means that the appendages were free to be used for different aims such as food collecting.

#### Relationship between brim and appendages

In general, the morphology of the arthropod appendages directly influences the method of feeding. The combination in *Ityophorus* of long legs surrounded by a brim forming a long "skirt" should have been of significance for the mode of life. As described above, the two sets of terrace lines are restricted to the edge of the brim, where the steep sides of each set face the other set (Figures 3H, 5). The lower set of terrace lines should have prevented the animal from sliding laterally outwards (Schmalzfuss, 1981), while the inner set would hinder extensive sinking into the substrate.

When an appendage scratched the substrate in one direction (Figure 5; black arrow with A), the body would be subjected to a pull in the opposite direction (Figure 5; black



**Figure 5.** Schematic drawing of transversely sectioned cephalon (black arrow in top of the figure) with inferred appendage, showing the relationship of the action and reaction mechanics between the exoskeleton and the substrate when the animal was scratching. The rectangle shown in the right of the figure is the magnified cephalic rim with substrate. For more details, see text. Black arrow with A means the vector of action from exoskeleton to the substrate, black arrow with R of reaction from the latter to the former.

arrow with R). This is determined by simple physical rules. Scratching or burrowing leg movements may also tend to pull animal downwards into the substrate. In *Ityophorus*, the terrace lines on the cephalic rim would hinder the head shield from sliding sideways or downwards (Figure 5; see magnification in left rectangle). Thus, for as long as the animal kept scratching, it could presumably move along inclined walls in a cavity. This mode of behaviour would work on a gel-like or sticky substrate such as a bacterial mat, the existence of which is suggested by the geological setting. Such a mode of life must require one more important factor, a low weight of the animal. *Ityophorus* was indeed unusually small and light. Therefore, I conclude that *Ityophorus* was most probably adapted to cavities coated with microbial mats. Some examples are known from Recent cavity-dwelling arthropods such as isopods which feed directly on fungi and bacteria (Sarbu and Popa, 1992).

#### Epilogue

The Late Ordovician trilobite *Ityophorus undulatus* appears to have had a set of morphological characters characteristic of cavity dwellers, such as reduced eyes, long appendages relative to the body length, considerable dwarfing, and possible heterochronic development, which is most likely to be progenesis. The supposed ancestral group of the Ityophorinae, the Loganellidae, is thought to be extinct before the Cambrian-Ordovician transition. A relict group might have persisted into the Ordovician by "progenetic evolution", and later adapted into a cryptic life. This is the first report that tries to interpret a phylogenetically relict fossil group as cryptic animals.

A Devonian proetid genus, *Denemarkia* (see Moore, 1959, O397; Snajdr 1980, p. 146, pl. 37), was a possible cavity dweller (Alberti, 1969, p. 336) with an overall morphology similar to *Ityophorus*. Taphonomical evidence showing the entombment of *Denemarkia* specimens in a cavity is available (such an occurrence pattern is not illustrated so far but a slab showing such a situation is stored in National Museum, Czech Republic, museum number L 16634). *Denemarkia* is known from the Devonian Koněprusy Limestone in Czech Republic (Šnajdr, 1980) and the Kess Limestone in Morocco (Alberti, 1969). Both limestone units are of the carbonate mud mound type of buildups. Interestingly, shared characters between *Denemarkia* and *Ityophorus*, such as fairly vaulted cephalon (see Moore, 1959, fig. 302-1b), distinct cephalic rim with wide cephalic doublure, lacking mesial embayment for the hypostomal suture (see Snajdr, 1980, pl. 27, fig. 9), a combination of which is quite rare in proetids, and less developed eye, are a fairly unique morphological combination in trilobites. A major morphological difference between the two is that the dorsal exoskeleton of *Denemarkia* is fairly rich in tubercles, whereas *Ityophorus* is smooth, and this can be explained as a result of adaptation to cavities as discussed previously. Repeated body modifications into ityophorid-like morphology from completely different clades means that there was a general capacity in the Trilobita to evolve in this direction.

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